Flavor Avoidance Learning and Its Implications in Reducing Strychnine Baiting Hazards to Nontarget Animals

ABDERRAHIM EL HANI,*† J. RUSSELL MASON,‡[1] DALE L. NOLTE§ AND ROBERT H. SCHMIDT¶

*Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322; †Ministry of Agriculture,
Rabat, Morocco; ‡U.S. Department of Agriculture, Animal and Plant Health Inspection Service/Wildlife
Services, National Wildlife Research Center, BNR-163, Utah State University, Logan, UT 84322-5295;
§U.S. Department of Agriculture, Animal and Plant Health Inspection Service/Wildlife Services,
National Wildlife Research Center, 9701 Blomberg Street, SW, Olympia, WA 98512;
and ¶Department of Fisheries and Wildlife, Utah State University,
Logan, UT 84322-5210, USA

EL HANI, A., J. R. MASON, D. L. NOLTE AND R. T. SCHMIDT. *Flavor Avoidance learning and its implications in reducing strychnine baiting hazards to non-target animals.* PHYSIOL BEHAV **64** (5) 585–589, 1998.—In reforested areas, underground strychnine baiting to control pocket gophers (*Thomomys mazama*) poses a hazard to golden mantled ground squirrels (*Spermophilus lateralis*) and yellow pine chipmunks (*Eutamias amoenus*). We designed this study to assess whether: 1) chemical insensitivity to bitter tastes might explain the ingestion of strychnine; 2) pocket gophers would avoid four bitter-tasting compounds: quebracho (QUEB), sucrose octaacetate (SOA), quinine hydrochloride (QHCl), and denatonium benzoate (DB); and 3) nontarget species could be trained to avoid strychnine paired with the most aversive compound. Our results showed that while all species readily consumed strychnine, the nontarget species could be conditioned to avoid it. Moreover, while high (0.1%) concentrations of DB, quinine hydrochloride, and quebracho reduced consumption by pocket gophers, 0.05% DB was inoffensive. Nontarget animals readily avoided 0.05% DB, and avoidance was stronger after conditioning. Together, our results suggest that all of the rodents tested are insensitive to strychnine, high concentrations of some bitter tastes may be effective pocket gopher repellents, and lower concentrations of DB may selectively repel nontarget animals from strychnine baits. © 1998 Elsevier Science Inc.

Baiting   Bitter   Chipmunk   Flavor   Gopher   Strychnine   *Thomomys*

PAIRING ingestion of a flavor with illness typically results in avoidance of the flavor. This effect has been called conditioned taste aversion or, more accurately, flavor avoidance learning (FAL). Because FAL is strong and occurs in only 1 trial, a number of attempts have been made to apply it as a psychophysical method. For example, Nowlis and Frank (27) and Nowlis et al. (28) used FAL to show that rats *(Rattus norvegicus)* and hamsters *(Mesocricetus auratus)* categorize tastants into sweet, sour, salty, and bitter. Mason et al. (23,24) used this method to demonstrate that generalization could be used to identify and mimic the flavor of strychnine and other rodenticides. Attempts also have been made to apply FAL as a predator management tool (14,15,6,13) and explain bait shyness (23,24,29,30,31).

In the Pacific Northwest, pocket gophers (*Thomomys mazama*) constitute a major problem to reforestation efforts (8,7). Underground strychnine baiting (5) is the most widely used method to control this species (3,22). However, this method poses a hazard to

golden mantled ground squirrel (*Spermophilus lateralis*; ground squirrels) populations and yellow pine chipmunks [*Eutamias amoenus*; chipmunks; (2,9 L. Nolte, J. R. Mason and R. H. Schmidt, manuscript in preparation]. One plausible explanation for the effectiveness of strychnine against gophers, as well as the nontarget effects on ground squirrels and chipmunks, is that all three species are primarily herbivorous, and herbivores are often insensitive to bitter substances or unable to detect them (4).

In Experiment 1, we assessed whether pocket gophers would avoid the flavor of four bittering agents: quebracho, sucrose octaacetate, quinine hydrochloride, and denatonium benzoate in the absence of training. We chose this palette of bitters because each of these substances is aversive to at least one species of rodent {rats, Stewart et al. (31), Mason et al. (23,24); voles [*Microtus pennsylvanicus*], Swihart (32); guinea pigs [*Cavia porcellus*], Jacobs (18), Nolte et al. (26); mice [*Peromyscus melanotis*], Glendinning (11)}. Also, there is evidence that strain and species dif-
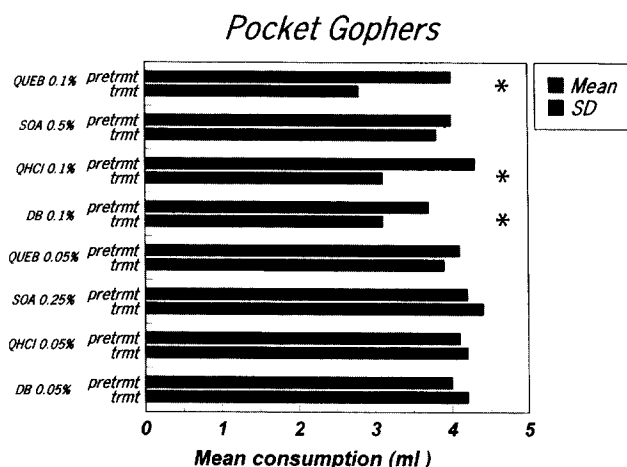
FIG. 1. Mean consumption (mL + SD) by pocket gophers of tap water (pretrmt) and tastants (trmt) during Experiment 1. Abbreviations: QUEB = quebracho; SOA = sucrose octaacetate; QHCl = quinine hydrochloride; DB = denatonium benzoate. Asterisks indicate significant differences ($p < 0.05$).

ferences in bitter perception and/or tolerance exist among mice (10), and we speculated that the same might be true for other species as well. Finally, we aimed to determine whether pocket gophers might be indifferent to substances that ground squirrels and chipmunks avoid.

In Experiment 2, we investigated whether ground squirrels, chipmunks, and pocket gophers would avoid strychnine, denatonium benzoate, and sucrose octaacetate when these substances were used as conditional stimuli in FAL. We tested denatonium benzoate because it was the most aversive, and sucrose octaacetate because it was not an aversive tastant in Experiment 1. In addition to evaluation of conditioning per se, we also tested for generalization among these stimuli. In Experiment 3, we assessed whether animals trained to avoid denatonium benzoate would avoid strychnine bait treated with this compound.

MATERIALS AND METHODS

Experiment 1

Subjects. We live-trapped 36 male and 32 female pocket gophers (76 ± 12 g [[· ± SD]]) in western Washington. Animals were individually caged (30 × 18 × 25 cm) under a 0:24 light:dark cycle at 22°C, and permitted free access to rodent chow (Purina Rodent chow), apples, and water.

Stimuli. Sucrose octaacetate (SOA; CAS no. 126–14-7), denatonium benzoate (DB; CAS no. 3734–33-6), and quinine hydrochloride (QHCl; CAS no. 6119–47-7) were purchased from Sigma Chemical Company. We obtained quebracho (QUEB; CAS no. 4850–21-9) from Van Dyke Supply Company (Woonsocket, SD, USA).

Procedure. During a 7-day pretreatment, we gave animals tap water (in 10-ml plastic syringes fitted with metal sipper tubes) for 30 min in the morning and 60 min in the afternoon (28,26). We then assigned animals to eight groups based on the average amount of water consumed during the 30-min morning periods on Days 4–7, with animals having the highest and lowest consumption assigned to the first group, those with the second highest and second lowest consumption assigned to the second group, and so forth. Throughout the experiment, chow was freely available.

Approximately equal numbers of males and females were assigned to each group.

On Day 8, we presented each group with a different tastant in aqueous solution. Group 1 received 0.1% (mass/volume, m/v) QUEB; group 2, 0.5% (m/v) SOA; group 3, 0.1% (m/v) QHCl; and group 4, 0.1% (m/v) DB. Groups 5–8 were given 0.05% (m/v) QUEB, 0.25% (m/v) SOA, 0.05% (m/v) QHCl, and 0.05% (m/v) DB, respectively. We selected stimulus concentrations on the basis of previous work (26,10,32). Concentrations were chosen to maximize usefulness as taste stimuli and minimize postingestive consequences.

Analysis. We evaluated drinking in a two-factor fixed effects ANOVA. The between measures factor in this ANOVA was groups (eight stimulus concentrations), and the repeated factor was period (pretreatment versus treatment). Mean pretreatment and mean treatment consumption was the dependent variable. We used Tukey post hoc tests (36) to isolate significant differences among means ($p < 0.05$).

Experiment 2

Subjects. We live-trapped seven male and seven female ground squirrels (192.2 ± 32 g), and nine male and seven female chipmunks (49 ± 4.2 g) in eastern Washington. Animals were individually caged (cage dimension 30 × 18 × 25 cm) under a 12:12 light:dark cycle, at 22°C. Fourteen male and 10 female pocket gophers (80.7 ± 10.4 g) were trapped and maintained under the conditions previously described.

Stimuli. Strychnine (CAS no. 1421–86-9, Sigma), SOA, and DB served as stimuli

Procedure. We adapted each species to water deprivation and assigned animals to groups as previously described. Approximately equal numbers of males and females were assigned to each group. On the day of treatment, we exposed group 1 (four ground squirrels, five chipmunks, and six gophers) to 0.05% SOA, group 2 (four ground squirrels, five chipmunks, and six gophers) to 0.05% DB, and group 3 (six ground squirrels, six chipmunks, and 12 gophers) to 0.008% strychnine. The concentration of strychnine was selected because of its use in other studies as a reliable conditional stimulus (31,23,24). We used SOA and DB as conditional stimuli because DB was and SOA was not aversive in Experiment 1. After at least 1 ml was consumed, or 30 min had passed, we gave each animal an intraperitoneal (i.p.) injection of 0.3 m lithium chloride (LiCl; 10 mL/kg) to induce gastrointestinal malaise. On the 2 days following treatment, we gave animals free access to rodent chow and water to permit recovery from malaise. We reinstated water deprivation at 0600 hours on the second day. On each of the next 3 days (posttreatment days 3–5), all animals were presented with strychnine, SOA, and DB during the 30-min morning drinking periods, and consumption was recorded.

Analysis. A three-factor ANOVA was used to assess consumption. The independent factors were species (three levels) and compounds (three levels). The repeated factor was days. The final pretreatment day, the treatment day, and each of the 3 posttreatment days were considered as levels of the repeated factor.

Experiment 3

Subjects. We trapped and maintained six male and four female pocket gophers (86.7 ± 10.4 g), and seven male and three female chipmunks (48 ± 3.4 g) under the conditions previously described. Ground squirrels were not tested because animals started hibernation in early fall and became unavailable for capture.

Stimuli. Strychnine (0.5%) and DB (0.05%) served as stimuli. The concentration of the former is commonly used for pocket gopher control. The latter substance was selected because it was

Generalization; Pocket Gophers
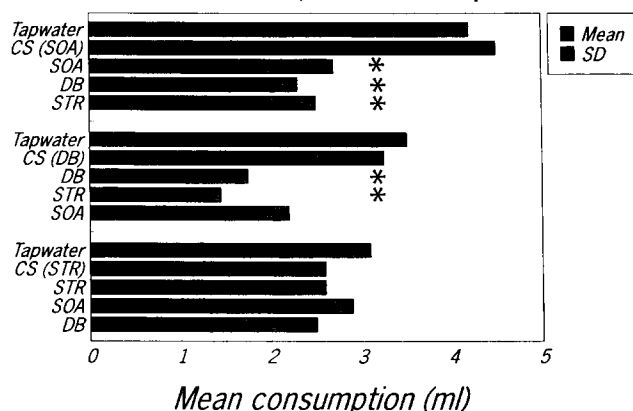

Mean consumption (ml)

FIG. 2. Mean consumption (mL) of tap water, conditional stimuli (CS) prior to injection with LiCl and subsequent generalization to other stimuli by pocket gophers in Experiment 2. Abbreviations: SOA = sucrose octaacetate; DB = denatonium benzoate; STR = strychnine. Asterisks indicate significant differences ($p < 0.05$).

the strongest and most reliable generalization stimulus in Experiment 2. We prepared the baits by treating oat groats (Pocatello Supply Depot, Pocatello, ID, USA) with strychnine and DB dissolved in diethyl ether. Treated baits were placed under a fume hood and exposed to air for 36 h to assure evaporation of the ether.

Procedure. After a 2-week period of adaptation, we randomly assigned animals to experimental and control groups ($n = 5$ animals/species/group). On the day of treatment, experimental animals were exposed to an oat groat bait containing 0.05% DB. This concentration was accepted by gophers but avoided by ground squirrels and chipmunks in Experiment 2. Control animals were exposed to untreated oat groats. Neither bait contained strychnine. Experimental (DB) animals then received an i.p. injection of 0.3 M LiCl (10 mL/kg) while control animals were given an injection of physiological saline (10 mL/kg). After 2 days of free access to food and water, animals were food deprived for 12 h, and then offered a choice between plain rodent chow and a 0.5% strychnine bait also containing 0.05% DB. Consumption was measured after 6 h.

Analysis. A three-factor ANOVA was used to evaluate the results. The independent factors were species (two levels) and treatments (two levels), while the repeated factor was food type (two levels).

RESULTS

Experiment 1

There was an interaction between chemicals and periods [$F(7, 60) = 6.74$; $p < 0.00001$[. Pocket gophers drank less 0.1% DB, 0.1% QHCl, and 0.1% QUEB ($ps < 0.01$) than plain water (Fig. 1).

Experiment 2

The three-way interaction among species, flavors, and days was significant [$F(16, 176) = 2.17$; $p < 0.007$]. On the day of conditioning, pocket gophers drank the same amount of SOA and DB (p-values > 0.22) as they did tap water during pretreatment (Fig. 2). Chipmunks (Fig. 3) and ground squirrels (Fig. 4) drank less DB

than tap water (p-values < 0.03), but not SOA ($ps > 0.8$). After conditioning, ground squirrels and chipmunks avoided ST, DB, and SOA (p-values < 0.01). Pocket gophers continued to drink the same amount of strychnine as before conditioning ($p > 0.42$), although cosumption of DB and SOA was reduced (p-values < 0.01).

During generalization trials, pocket gophers given SOA as the conditional stimulus also avoided DB and strychnine (p-values < 0.01; Fig. 2). Gophers given DB as the conditional stimulus only generalized avoidance to strychnine (p-values < 0.02). When strychnine served as the conditional stimulus, consumption was the same on treatment and posttreatment days (p-values > 0.22). Chipmunks showed broad significant generalization (p-values < 0.05) regardless of the conditional stimulus (Fig. 3). For ground squirrels, similiarly broad generalization was obtained when SOA and DB served as conditional stimuli (Fig. 4). Strychnine was a poor conditional stimulus, and avoidance generalized ($p < 0.05$) to SOA alone (i.e., significant generalization was not observed toward strychnine or DB). For all three species, the strongest generalization occurred from SOA to DB.

Experiment 3

There was a significant interaction between species and food type [$F(1, 16) = 6.7$; $p < 0.019$]. Chipmunks consumed less strychnine-DB adulterated oats than rodent chow ($p < 0.05$; Fig. 5). Pocket gophers ate similar amounts of untreated and treated food in both the treatment and control groups (p-values > 0.25).

Discussion and Management Implications

Our results show that pocket gophers avoid 0.1% QUEB, QHCl, and DB in the absence of training (i.e., consumption was reduced even on the first exposure). This suggests that avoidance of these substances was at least partly sensory in nature. While herbivores tend to be insensitive to bitter substances (12,4), these data suggest that, at sufficiently high concentrations, QUEB, QHCl, and DB might serve as repellents. SOA, however, was readily accepted by pocket gophers at both of the concentrations tested. Rats (20,16), guinea pigs (18), and mice (*Peromyscus* spp.;

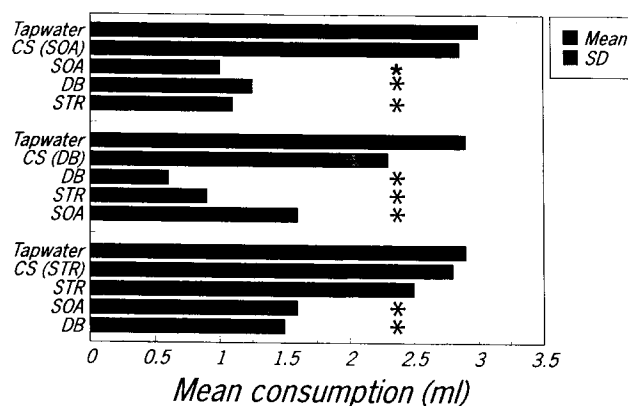## Generalization; Yellow Pine Chipmunks

Mean consumption (ml)

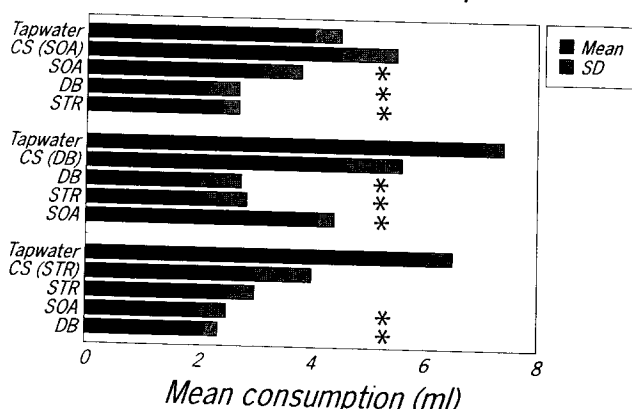FIG. 3. Mean consumption (mL) of tap water, conditional stimuli (CS) prior to injection with LiCl, and subsequent generalization to other stimuli by chipmunks in Experiment 2. Abbreviations: SOA = sucrose octaacetate; DB = denatonium benzoate; STR = strychnine. Asterisks indicate significant differences ($p < 0.05$).

FIG. 4. Mean consumption (ml) of tap water, conditional stimuli (CS) prior to injection with LiCl, and subsequent generalization to other stimuli by ground squirrels in Experiment 2. Abbreviations: SOA = sucrose octaacetate; DB = denatonium benzoate; STR = strychnine. Asterisks indicate significant differences ($p < 0.05$).

10) also readily consume SOA. Other putatively bitter tastants to which some rodents appear indifferent include naringin (26), pyrrolizidine, digitoxin, and monocrotaline (12).

Ground squirrels and chipmunks discriminate between tap water and 0.05% DB, while pocket gophers do not. The difference in taste response between these species may reflect differences in feeding guilds. Pocket gophers are strict herbivores, while chipmunks and ground squirrels are relatively omnivorous (25). Interspecific differences in taste response have been described elsewhere (19,30,4,11). The physiological mechanisms underlying these differences remain obscure.

After conditioning, ground squirrels and chipmunks avoided all of the taste stimuli, particularly DB. Pocket gophers, however, failed to avoid strychnine, regardless of the method of stimulus presentation (fluid or food). This result is consistent with previous

work. For example, Howard et al. (17), Marsh and Howard (22), Willis (35), and Tickes et al. (33) reported that gophers continue to ingest strychnine bait even after they have experienced toxicant-induced convulsions and despite their ability to learn avoidance of the bait, per se (22). Several plausible explanations for these data can be offered. First, strychnine could interact with LiCl and hinder conditioning. Second, gophers may be unable to detect strychnine as a sensory stimulus, even though they can detect and avoid SOA and DB. Conceivably, conditioning with one of these substances might enhance detection of strychnine via some attentional mechanism. This possibility is consistent with our finding that the order of stimulus presentation influenced generalization. For example, when SOA was the conditional stimulus, all species avoided DB, but when DB was the conditional stimulus, they all were indifferent to SOA. Similarly, when pocket gophers and ground squirrels were conditioned to avoid DB, animals subsequently avoided strychnine; however, when strychnine served as the conditional stimulus, generalization to DB did not occur.

Underground baiting with 0.5% strychnine oat bait is the most commonly used method to control pocket gophers in reforested areas (3,7,21). However, this method can be hazardous to nontarget species (2; El Hani, A., D. L. Nolte, J. R. Mason, R. H. Schmidt, manuscript in preparation). The results of the present experiments suggest several possible means to reduce hazards to nontarget species. First, 0.1% QHCl and 0.1% DB may be useful as nonlethal repellents to reduce pocket gopher damage to seedlings. Because both of these compounds are water soluble, it is possible that both can be translocated by plant tissues. When sprayed on apple twigs at 0.03%, DB was ineffective in deterring browsing by mule deer [Odocoileus hemionus; (1)], Conceivably, a higher concentration (e.g., 0.1% DB) could confer some protection. Second, both ground squirrels and chipmunks avoided 0.05% DB in the absence of training. This suggests the possibility that 0.05% DB might be added to strychnine gopher baits as a method to reduce nontarget hazard. Finally, FAL might be used to further reduce bait consumption by nontarget animals. Prebaiting above ground with baits containing 0.05% DB and LiCl could be used to produce learned avoidance of DB-treated baits. During subsequent baiting, both learned and unlearned avoidance of DB would act to
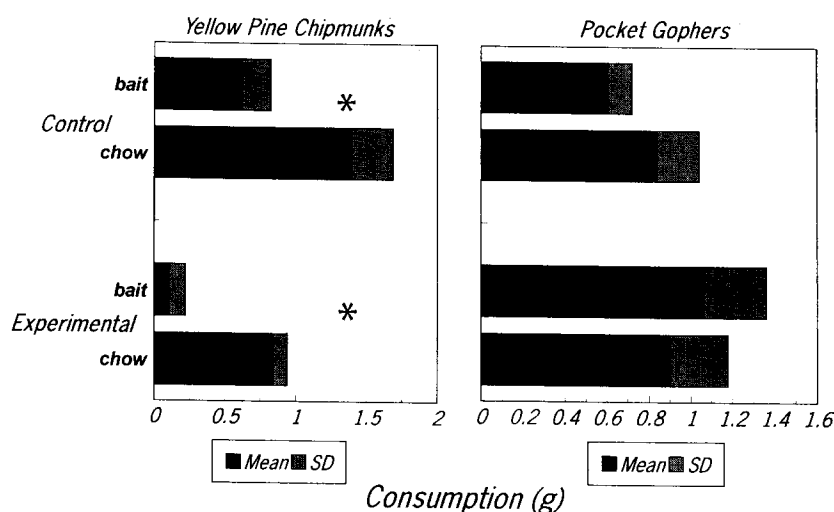

FIG. 5. Mean consumption (g) of oats adulterated with denatonium and strychnine (bait) or rodent chow by yellow pine chipmunks and pocket gophers in Experiment 3. Asterisks indicate significant differences ($p < 0.05$).

protect chipmunks and ground squirrels from incidental consumption of strychnine baits.

SUMMARY

Strychnine baiting to control pocket gophers is a common practice that may pose a hazard to nontarget species, including chipmunks and ground squirrels. We designed the present experiments to test whether species differences in taste sensitivity could possibly represent a strategy to reduce or eliminate this hazard. Our results suggest that denatonium benzoate is offensive to nontarget species, but not to gophers. Conditioning can be used to

enhance this differential response. The practical implication of these findings is that denatonium might be used to reduce the nontarget hazards associated with strychnine baiting programs.

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